# KARYOLOGICAL HETEROGAMETY OF DEEP-SEA FISHES

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ABSTRACT

Among 25 deep-sea fish species karyologically investigated, digamety is confirmed in 12. Observations were based on the consistent appearance of heteromorphic chromosome pairs, of asymmetrical and atypically behaving "sex" bivalents, and of two different chromosome counts from metaphase II. The occurrence of such digamety in other lower vertebrates is discussed. It occurs more frequently among teleostean fishes and other lower vertebrates than previously expected.

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## Introduction

Probable cytological digamety has been repoorted in several fishes before 1945 (Geiser, 1924; Foley, 1926; Vaupel, 1929; Ralston, 1933, 1934; Bennington, 1936; and Barigozzi, 1937). But its occurrence was questioned by Friedman and Gordon (1934), Makino (1934a, b), and Wickbom (1941, 1943), who doubted that atypical bivalency indicated heterogamety and denied any evidence of cytological sex differentiation. In the gwyniad *Coregonus lavaretus,* Svärdson (1945) discovered that most karyotypes of blastomeres from about half of the embryos examined included a supernumerary chromosome. But this chromosome was absent in testicular preparations from adult males. Consequently, he claimed that this fish was female heterogametic and that the supernumerary probably was the female-determining chromosome. In two specialized perciform fishes, *Mogrunda obscura* and *Cottus pollux,* Nogusa (1955, 1957) described possible XY male heterogamety from observations of heteromorphic and heteropycnotic bivalents. Lieder (1963) observed a non-paired chromosome "fragment" in the percid *Acerina cernua* and a satellited chromosome in the percid *Perca flaviatilis* and the freshwater eel *Anguilla anguilla,* and suggested that the "fragments" or "satelliteds" might be male-determining Y-chromosomes. He cautioned, however, that the partner of the satellited chromosome was probably not an X-chromosome but rather an autosomal homologue, indicating a "YO" sex type. Chen and Ebeling (1966) reported heteromorphic mitotic X and Y chromosomes and their presumed bivalent showing end-to-end chromatic association from all specimens of the deep-sea fish *Bathylagus wesethi* examined. Its heterogamety was further substantiated by the occurrence of two X's in tetraploid cells, probably from testicular supporting tissue, and by the occurrence of two dissimilar counts from secondary spermatocytes, one including, the other excluding this remarkably large chromosome. Moreover, by examining different somatic tissues (gill epithelium, spleen and kidney) as well as gonads, Chen and Ebeling (1968) reported cytological heterogamety in the mosquitofish *Gambusia affinis,* in which the female karyotype is characterized by a large metacentric, which, however, is absent in the male. We concluded that the mosquitofish is female-heterogametic of the WZ-ZZ sex type.

The cytology of deep-sea fishes, which are adapted to a remote, cold, dark, hyperbaric, relatively impoverished environment, has been little studied. Adaptation to such a stress condition may include various atypical cytological expressions (cf. Stebbins, 1966). The present paper reports the probable occurrence of cytologically expressed digamety among 25 selected deep-sea fishes.

## Materials and Methods

Specimens were captured off the coast of southern California as far as Guadalupe Island, Mexico. Most tissues were first placed in 0.9 percent sodium citrate for about 20 minutes, then fixed in 1 : 3 acetic alcohol, and stored under refrigeration. A few live specimens of *Lampanyctus ritteri, Triphoturus mexicanus,* and *Bathylagus ochotensis* were injected intra-peritoneally with 0.05 percent colchicine. They were maintained for about two hours at 5°C, then killed and fixed. These colchicinized specimens provided many good metaphase plates. In total, about one thousand preparations from 114 specimens were examined or about 40 preparations from 2-10 specimens per species. Tissues for the squash preparations were mainly testicular; the only female tissues observed were ovarian metaphase plates from two halfgrown females of *Lampanyctus ritteri.* Occasionally kidney tissue provided good metaphase plates. Tissues were usually stained with aceto-orcein. Photomicrographs of the preparations were taken under both bright and phase-contrast optics.

## Observations

The 25 deep-sea fish species are grouped according to their ordinal affinities: (1) the generalized salmoniform family Bathylagidae, (2) the related family of hatchetfishes, Sternoptychidae, (3) the evolutionarily intermediate myctophiform families of lanternfishes, Neoscopelidae and Myctophidae, and (4) the more specialized pre-percoid beryciform families Melamphaidae and Anoplogasteridae.

A). BATHYLAGIDAE. Bathylagids are typically mesopelagic (mid-depth) fishes, which live between 100 and about 1000 meters in the open ocean. This family includes but three or four deep-sea mesopelagic genera (Cohen, 1964). Cosmopolitan *Bathylagus* contains five Californian species, four of which were

investigated (Figs. 1-10). Their diploid numbers range from 36 in *Bathylagus wesethi* to 64 in *B. stilbius*. Their male karyotype is unique in that its largest element, the presumed X chromosome, apparently comprises a considerable percentage of the total nuclear chromatin and lacks any homologue approaching it in size or morphology. Also, in all species but *wesethi,* it includes a series of very small chromosomes.

The presumed X is the largest metacentric chromosome in *B. wesethi, ochotensis,* and *milleri* but it is submetacentric in *stilbius* (Figs 1, 4-6). It is almost 1.5 times as long as the next largest chromosome in all but *ochotensis*. The presumed Y is acrocentric and is the smallest in *wesethi* but the next largest chromosome in the complements of *stilbius* and *ochotensis*. In *milleri,* which is the deepest-living species, it defies identification amongst the relatively large series of small dot-like chromosomes. In *wesethi* the sex bivalent, whose X and Y are associated end-to-end, appears satellited during metaphase I (cf. Chen and Ebeling, 1966, and Fig. 2). In metaphase II, two morphotypes, one with the "X" and the other without it, are readily identifiable (cf. Chen and Ebeling, 1966, and Fig. 3). Therefore, cytological male heterogamety is best demonstrated in this species. Although in the other species the karyotypes of secondary spermatocytes are unclear, their mitotic karyotypes and their presumed sex bivalent resemble those of *wesethi* (Figs. 7-10).

B). STERNOPTYCHIDAE. Hatchetfishes are small and common vertical migrators of the mesopelagic zone and like most such migrators have light organs, which are ventrally oriented. Four Californian species were studied. Their karyotypes are characterized by the presence of several chromosome pairs that are noticeably larger than the rest. Also, satellited pairs are relatively numerous, metacentric and submetacentric chromosomes dominate the complement, and heterochromatic bodies ("chromocenters") are distinctly expressed. Some of the larger chromosomes have many distinct heterochromatic bands throughout their length. In three species of *Argyropelecus,* sex chromosomes are not detectable. However, the diploid number of *Sternoptyx diaphana* is always 35 (Figs. 11, 12). The largest among five acrocentrics in the male complement is apparently unpaired. This may be the X of an XX-XO sex type and is the fifth largest pair in the

complement. Among leptotene cells, an elongate deeply stained body, which morphologically resembles the unpaired "sex chromosome" from somatic cells, is presumably a heterochromatic sex element (Fig. 13) but is not observable, however, during later stages of meiosis. Occasionally, one to four other "chromocenters" occur simultaneously, but invariably they disappear earlier than the morphologically persistent "sex element." In metaphase I the presumed univalent X, which is morphologically indistinguishable from the mitotic X, is clearly observable (Fig. 14). In metaphase II two morphotypes are detectable (Fig. 15): one with 18 elements and the other with 17 elements and presumably lacking the X chromosome.

c). NEOSCOPELIDAE and MYCTOPHIDAE. Comprising more than 30 genera (Fraser-Brunner, 1949; Bolin, 1959, 1966), lanternfishes are the most speciose and among the most abundant of all deep-sea fishes. Species are often distinguished by differences in the patterns of light organs on the flanks and belly. Of about 25 species that occur off California, 11 were investigated cytologically (Figs. 16-29). Most karyotypes are 2n=48, with acrocentric chromosomes predominating. The chromosomes are subequal in length, excepting the presumed X and one or two pairs. The times of occurrence and disappearance of heterochromatic bodies during prophase I distinguish taxonomic groups within the Myctophidae.

In *Scopelengys,* the only Californian representative of the relatively primitive Neoscopelidae, an atypically behaving bivalent, whose univalents are associated end-to-end, always occurs at the periphery of the metaphase plate; it is probably composed of subequal sex chromosomes (Fig. 17). In *Symbolophorus californiensis* of the family Myctophidae, a "sex bivalent" occurs at the periphery of the metaphase I plate. It is formed of two submetacentrics associated end-to-end and lags behind the others during anaphase I when its four arms are clearly detectable (Figs. 19-21). In the mitotic complement the first and fourth largest chromosomes are submetacentric and probably constitute the sex chromosome pair. In the above two species, a heterochromatic "sex element" (cf. *Sternoptyx diaphana*) is clearly detectable in leptotene cells (Figs. 16 and 18). In *Lampanyctus ritteri* the diploid number is 47 in males but 48 in females (Figs. 22, 23). The largest chromo-

some in the male complement is submetacentric but two such elements are observable in females. Probably, therefore, this species is male heterogametic of the XX-XO sex type. The X-chromosome usually but not always forms a characteristic Y-shaped trivalent, probably with a particular autosomal bivalent (Fig. 24). In anaphase I (Fig. 25) and metaphase II (Fig. 26) counts clearly are n=24 with the X and n=23 without the X. This asymmetry is also observable in the specialized deep-living species *Parvilux ingens,* whose diploid number is 49 in males (Fig. 27). During metaphase I the presumed X, which behaves differently and forms either a V or ring, may appear chromatically associated at both poles (Fig. 28). In metaphase II, counts were n=25 with the X and 24 without the X (Fig. 29).

D). MELAMPHAIDAE and ANOPLOGASTERIDAE. These families generally live at greater depths than the previous species. Like many bathypelagic fishes, they lack light organs and probably do not undergo extensive diurnal vertical migrations (Ebeling, 1962). Five melamphaids and monotypic *Anoplogaster cornuta* were studied (Figs. 30-35). The complement is made up either of subequal chromosomes in most species or of many very small acrocentric chromosomes in others, e.g., *Poromitra crassiceps.* Generally, acrocentrics dominate the complements, which are unusually variable in number among the genera. The heterochromatic bodies ("chromocenters") are clearly observable during early prophase I.

A heteromorphic "sex bivalent" is detectable in *Melamphaes parvus* and *Scopeloberyx robustus* (Figs. 34-35). In *Scopelogadus mizolepis bispinosus* a large, "lampbrush-like" bivalent, which differs from all others in having broad sections between its narrowed ends, is observable during zygotene and pachytene (Fig. 32). This "sex bivalent" is observable until metaphase I, shows no chiasmata, and may be associated end-to-end (Fig. 33). In the mitotic complement a pair of relatively long chromosomes obviously differ in length and probably constitute the heteromorphic sex pair (Fig. 30).

## Discussion

Cytologically expressed digamety had previously been reasonably verified in only seven of 260 teleost fishes hitherto investigated

(cf. Chen, 1967); however, the present results indicate that 12 of 25 deep-sea species have heteromorphic chromosome pairs, presumably of the XX-XY or XX-XO sex type. This disparity may be due primarily to technological difficulties in properly preparing slides for detailed study and to the generally small chromosome size of shallow-water fishes (Chen, 1967; Chen and Ebeling, 1968). Measuring five to six microns, however, most deep-sea fish chromosomes in mid-metaphase are two to three times as long as those of the shallow-water fishes which I and others have studied. Also the use of aceto-orcein has facilitated the present study because of its deep-staining affinity for chromatin. This allows examination of detailed chromosomal structures, which often are obscure in shallow-water fishes. Giemsa stains shallow-water fish chromatin very well, but is less effective than orcein for staining deep-sea fish chromatin.

Although in most deep-sea fishes, observations of sex chromosomes were made on testicular preparations only, abundant evidence substantiates the common occurrence of heteromorphic sex pairs: (1) these pairs are consistently observable among the tissues of different individuals, (2) males of some species have odd-numbered diploid counts, which were based on examination of at least three individuals from each species, (3) asymmetrical bivalents are always observable in metaphase I, and (4) the expected different haploid counts occur in MII in those species of the presumed XX-XO sex type. During metaphase I the atypically behaving "sex element" of *Scopelengys tristis* and *Parvilux ingens* always occurs outside the concentration of other bivalents in the metaphase plate. In *Scopelogadus m. bispinosus,* the only morphologically distinct chromosome during prophase I and metaphase I is probably the sex bivalent. In leptotene, a distinctly stained body, which is presumably of heterochromatic sex element and is easily distinguishable from "chromocenters," is observable in *Bathylagus milleri* (Fig. 10), *Sternoptyx diaphana, Scopelengys tristis, Symbolophorus californiensis,* and *Scopelogadus m. bispinosus* (Fig. 31).

The characteristic X of bathylagids is always distinctly longer than other chromosomes in the complement. This is substantiated in *Bathylagus wesethi,* whose two different types of metaphase II cells, one with and the other without this longest chromosome occur in equal frequency (Chen and Ebeling, 1966; and Chen,

1967). This strongly suggests that metaphase II cells without this element are not eliminated as zygotic lethals, i.e., that the chromosomal heteromorphy is an incident of isochromosomal fusion (Chen and Ebeling, 1966). Such a high frequency of deleterious cells would appear disadvantageous to this species and others in the family which have similar karyotypes. But, in fact, *Bathylagus stilbius,* whose karyotype is also characterized by the presence of a single distinctly hypertrophied chromosome in the complement, is one of the most abundant (i.e., most successful) mesopelagic deep-sea fishes in the eastern North Pacific Ocean. Therefore, it is most reasonable to assume that the large chromosome is the female-determining chromosome. The Y is interspecifically variable. It is the largest acrocentric chromosome in *Bathylagus ochotensis* but the smallest in *B. wesethi.*

Several investigators have suggested that intra-individual karyotypic polymorphism may commonly occur in shallow-water fishes (Ohno, Stenius, Faisst, and Zenzes, 1965; Ohno and Atkin, 1966; Beçak, Beçak, and Ohno, 1966).However, the intra- and inter-individual consistency of heteromorphic pairs observed in the present study seems unlikely to be the result of chromosomal interchanges. For example, not one bathylagid cell among about thirty specimens examined lacked the characteristic X chromosome. In the three hatchetfishes and lanternfishes of the presumed XX-XO sex type, the odd diploid counts in males were always based on more than 30 well spread metaphase plates. Also, the regular presence or absence of the large unpaired chromosome in secondary spermatocytes further substantiates their heterogamety.

Consequently, the occurrence of heteromorphic chromosome pairs may be much more widespread among teleosts than previously suspected. Also, the "Superorder" Teleostei is an evolutionarily diverse group, which has undergone extreme adaptive radiation. It is hardly conceivable that sex chromosomes remain primitively undifferentiated among its generalized and specialized species alike. Evidence of cytological digamety is accumulating in other lower vertebrates. For example, Nogusa (1957b) reported male heterogamey in the protochordate lancelet *Branchiostoma belcheri,* whose X is the largest and Y the smallest in the complement; Yosida (1957) observed it in the treefrog *Hyla arborea japonica;* and Gorman and Atkins (1966) and Gorman and Holzinger (1967) reported digamety in several species of the

lizard *Anolis,* whose multiple sex-chromosome mechanism consists of $X_1X_1X_2X_2$ in females and $X_1X_2Y$ in males.

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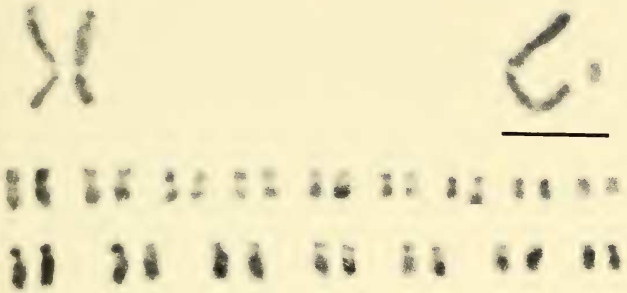
# PLATES

(All figures reproduced at same scale: $10\mu = 27$ mm)

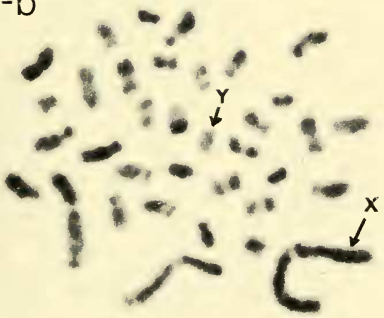
FIG. 1. Karyotype of *Bathylagus wesethi* (2n = 36). a. Idiogram. b. Metaphase plate corresponding to a. Presumed X and Y chromosomes are underlined in the idiogram and indicated with arrows in the metaphase plates. (All figures follow same citation as mentioned here. All figures: reproduced at same scale: $10\mu = 27$ mm)

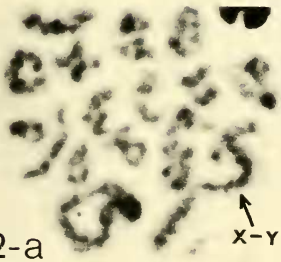
FIG. 2. Premetaphase I (a) and metaphase I (b) of *B. wesethi,* indicating the satellite-like "X-Y" bivalent (arrow).

1-a

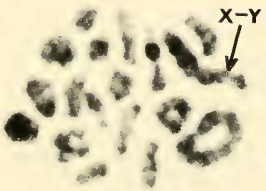


1-b




2-a




2-b

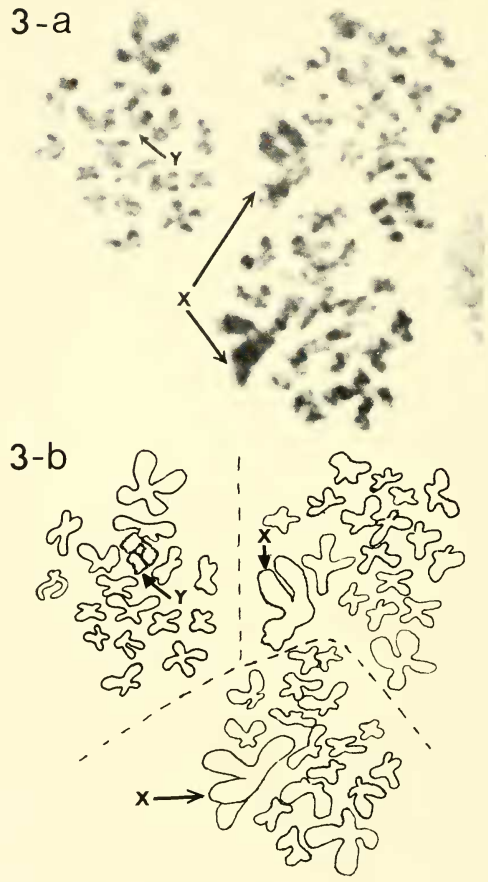



FIG. 3. Metaphase II of *Bathylagus wesethi*. N = 18 with the small "Y" (upper left) and with the large "X" (two cells at right).

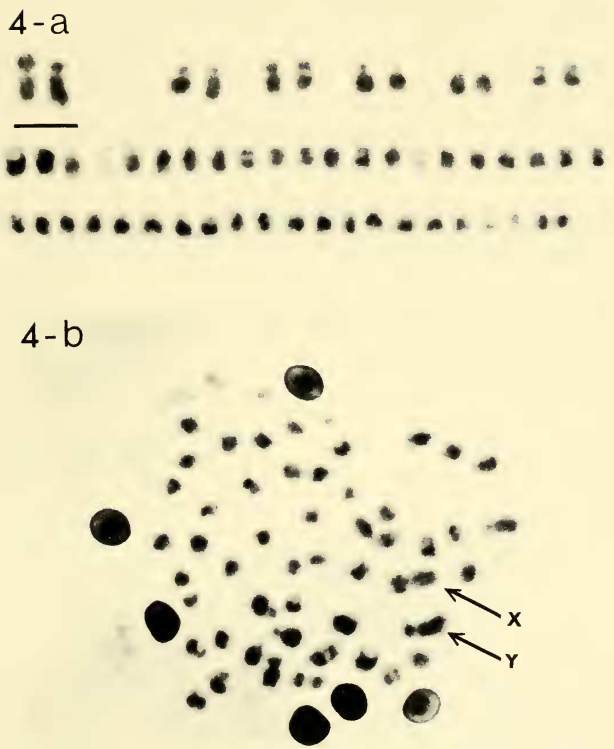



FIG. 4. Karyotype of *Bathylagus ochotensis* (2n = 54). a. Idiogram. b. Metaphase plate corresponding to a.

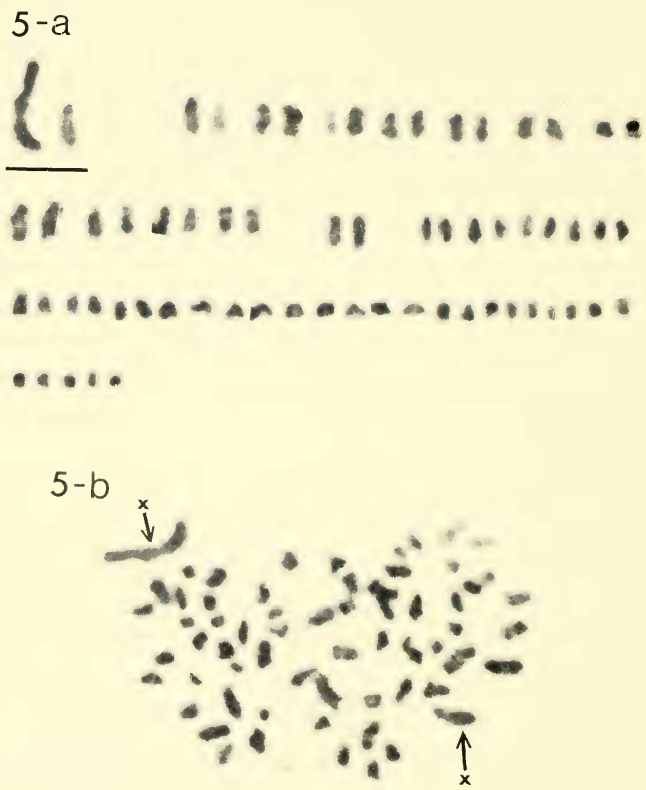



FIG. 5. Karyotype of *Bathylagus stilbius* (2n=64). a. Idiogram. Seven identifiable metacentric (M), 4 submetacentric (SM), and 1 acrocentric (A) pairs are placed separately. The rest are morphologically unidentifiable. b. Metaphase plate corresponding to a.

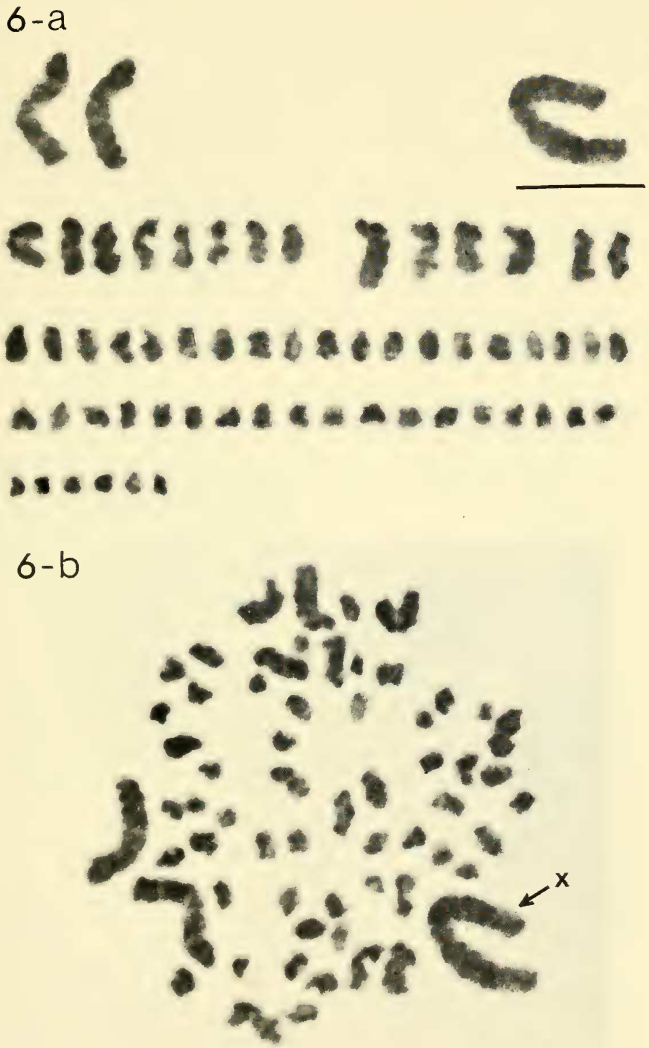



FIG. 6. Karyotype of *Bathylagus milleri* (2n=60). a. Idiogram. Morphologically identifiable autosomal pairs are placed separately. (cf. Fig. 5). b. Metaphase plate corresponding to a.

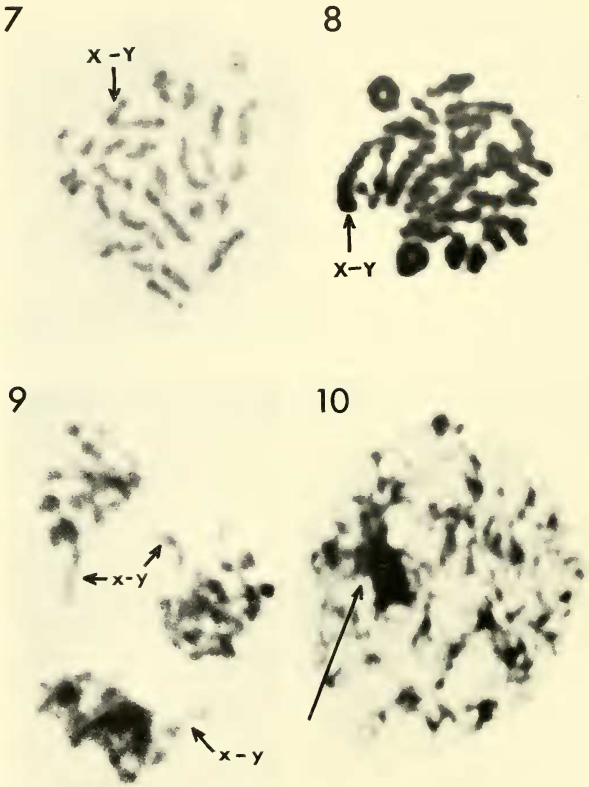



FIG. 7. Metaphase I of *Bathylagus ochotensis.*

FIG. 8. Metaphase I of *B. stilbius.*

FIG. 9. Metaphase I of *B. milleri.*

FIG. 10. Preleptotene of *B. milleri* showing the presumed heterochromatic sex element (arrow).

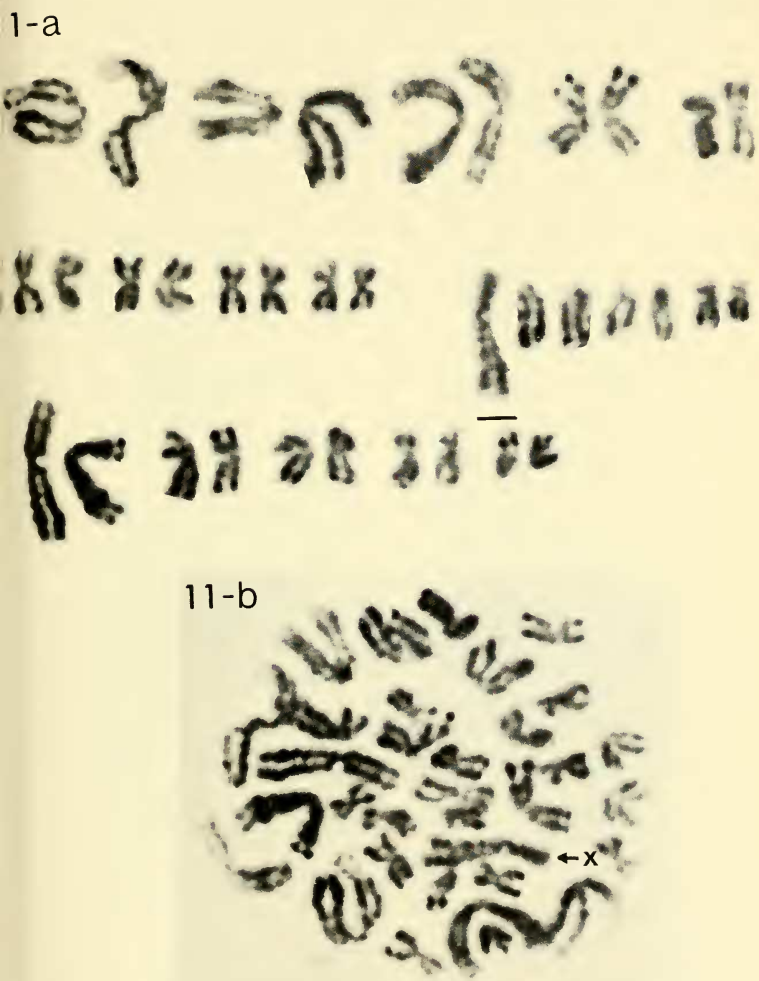



FIG. 11. Karyotype of *Sternoptyx diaphana* (2n=35). a. Idiogram. b. Metaphase plate corresponding to a.

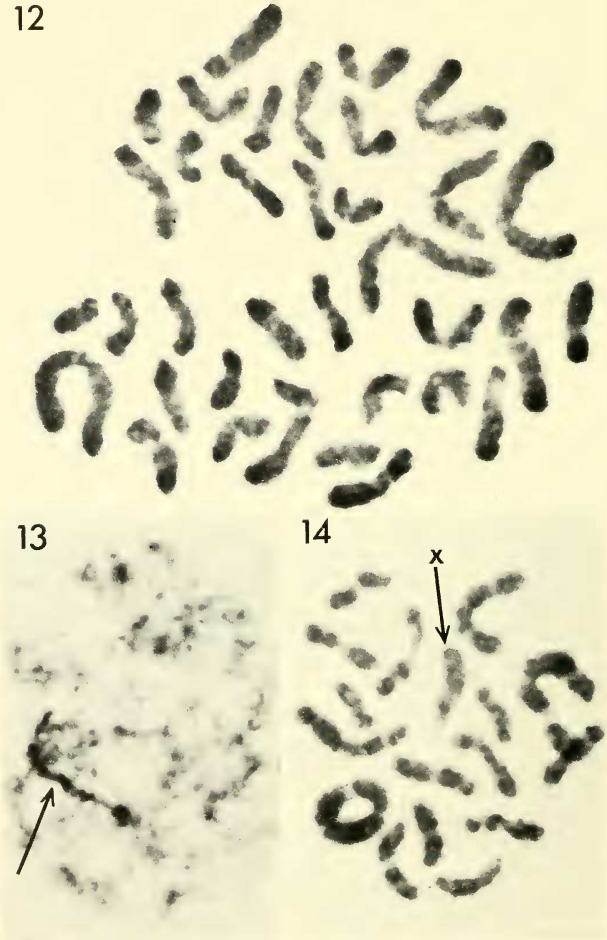



FIG. 12. Metaphase plate of *Sternoptyx diaphana*.

FIG. 13. Preleptotene of *Sternoptyx diaphana* showing the heterochromatic sex element (arrow).

FIG. 14. Metaphase I of *Sternoptyx diaphana* showing the univalent "X" (arrow).

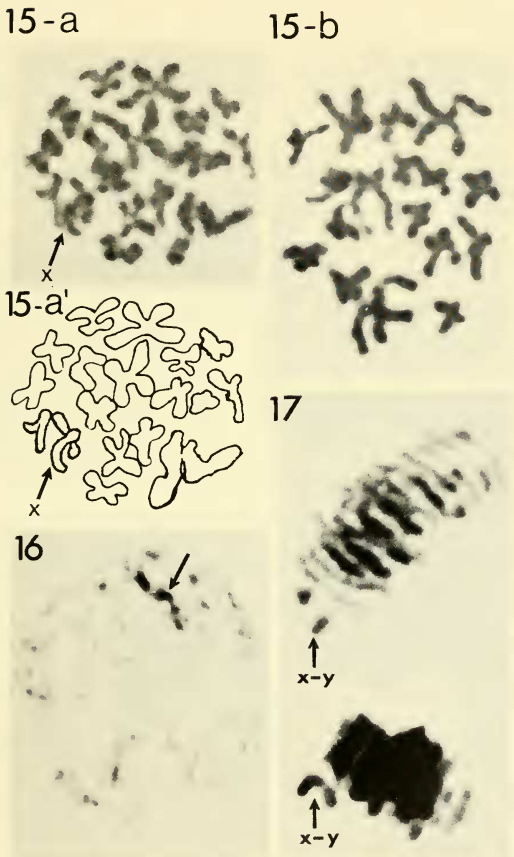



FIG. 15. Metaphase II of *Sternoptyx diaphana* showing 18 chromosomes (with the "X", a and a') and 17 (without the "X", b).

FIG. 16. Preleptotene of *Scopelengys tristis* showing the heterochromatic sex element (arrow).

FIG. 17. Metaphase I (sideview) of *Scopelengys tristis* (2n=48, n=24) showing atypically behaving presumed X-Y bivalent (arrows).

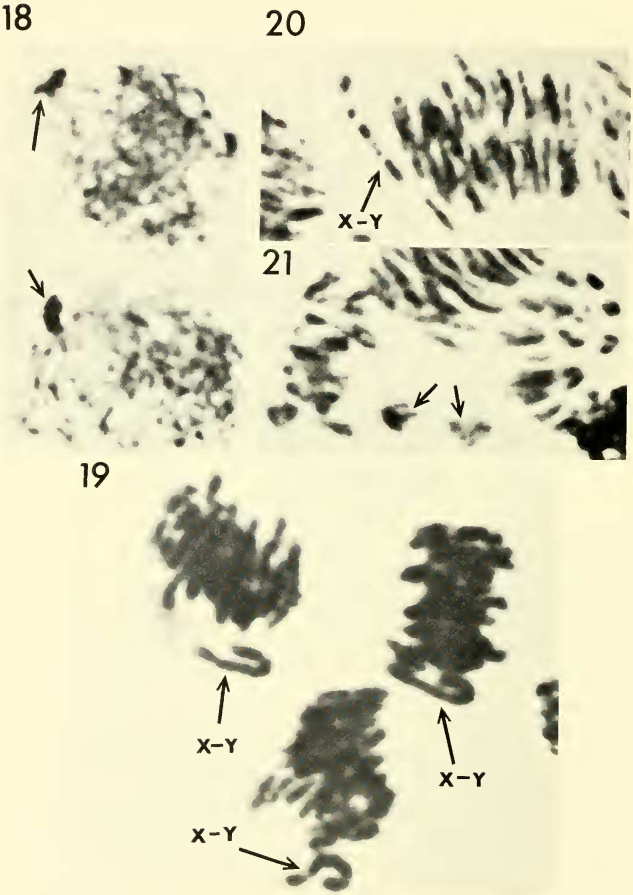



FIG. 18. Two leptotene cells of *Symbolophorus californiensis* (2n = 48; n = 24) showing the heterochromatic sex element (arrows).

FIG. 19. Metaphase I (sideviews) of *Symbolophorus californiensis* showing atypically behaving presumed sex bivalent (arrows).

FIG. 20. Early anaphase I of *Symbolophorus californiensis* showing the sex bivalent and its distinct heterochromatic bands (arrow).

FIG. 21. Anaphase I of *Symbolophorus californiensis* showing two lagging, presumed sex univalents (arrows).

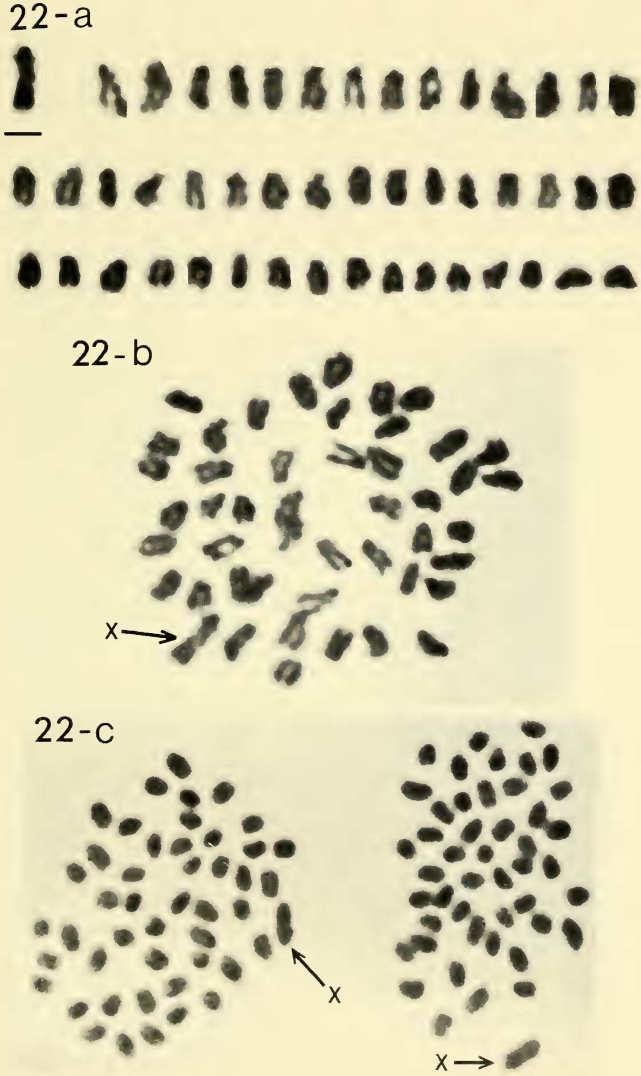
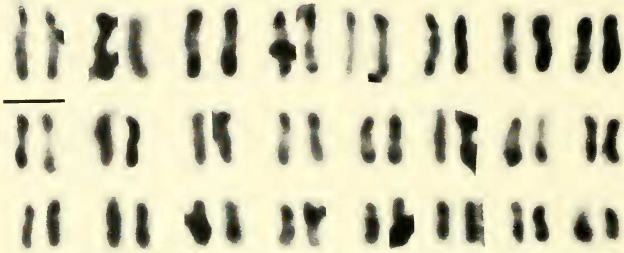
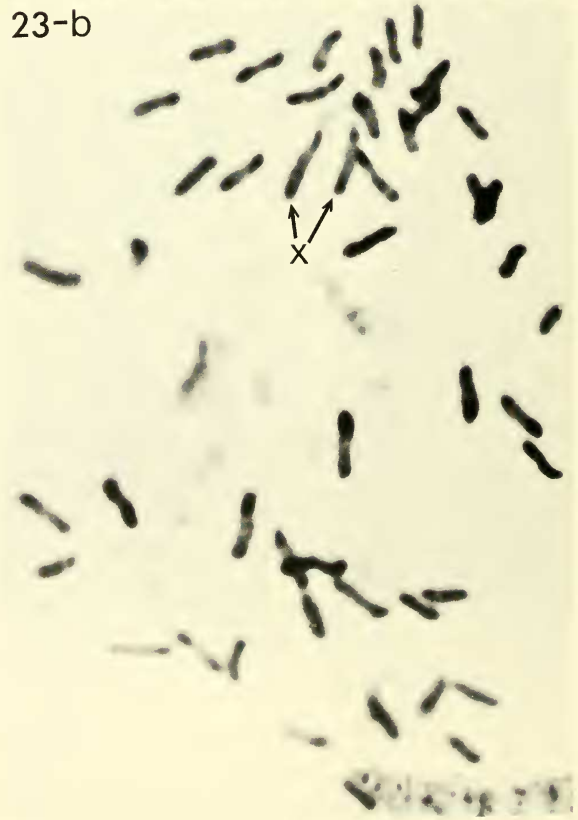



FIG. 22. Karyotype of male *Lampanyctus ritteri* (2n=47). a. Idiogram. b. Metaphase plate corresponding to a. c. Two late metaphase plates.

23-a



23-b



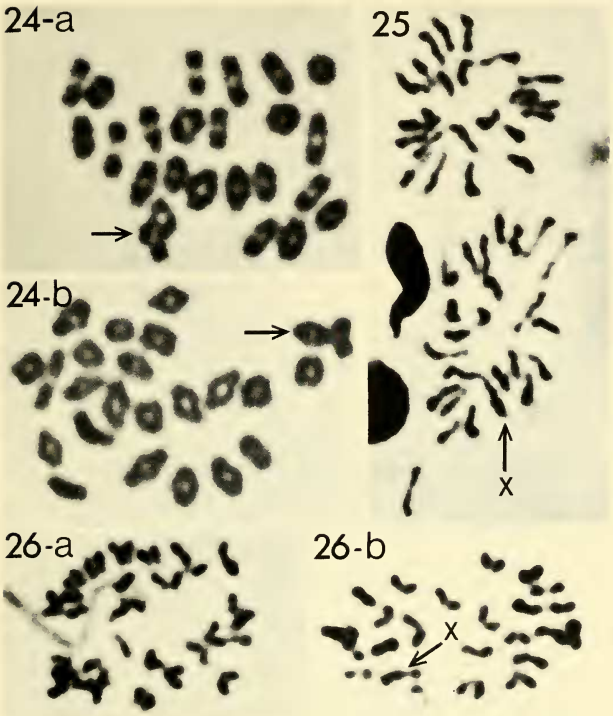



FIG. 23. Karyotype of female *Lampanyctus ritteri* (2n=48). a. Idiogram. b. Metaphase plates corresponding to a.

FIG. 24. Primary spermatocytes (MI) of *Lampanyctus ritteri* showing the "X"-autosome trivalent (a and b).

FIG. 25. Anaphase I of male *Lampanyctus ritteri* showing one (lower) with and the other (upper) without the "X" chromosome.

FIG. 26. Secondary spermatocytes (M II) of *Lampanyctus ritteri* showing: a, n=23 without, and b, n=24 with the "X".

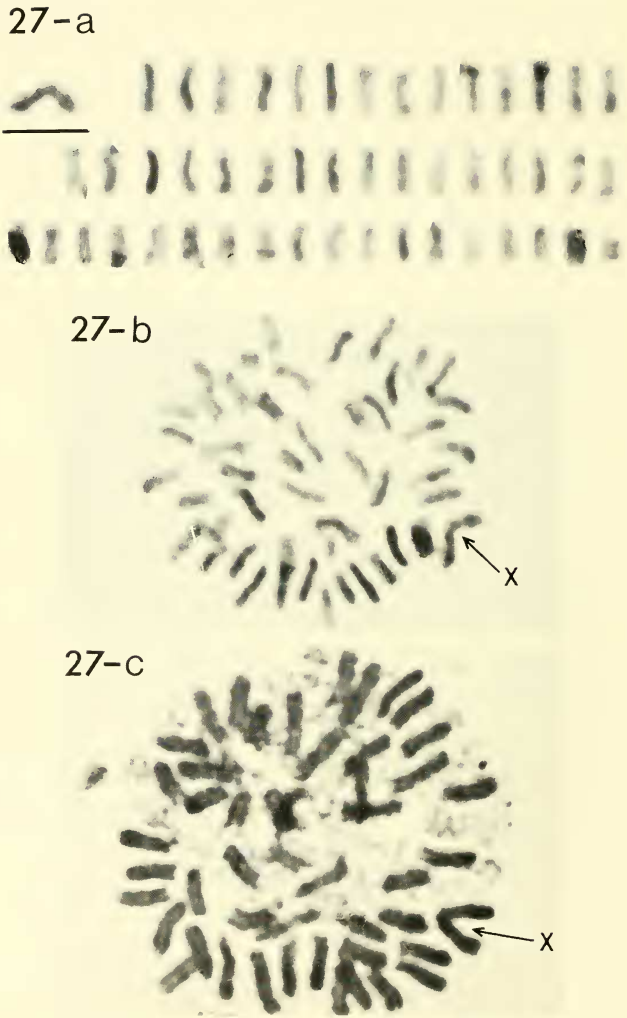



FIG. 27. Karyotype of *Parvilux ingens* (2n=49). a. Idiogram. b. Metaphase plate corresponding to a. c. Another metaphase plate showing the "X".

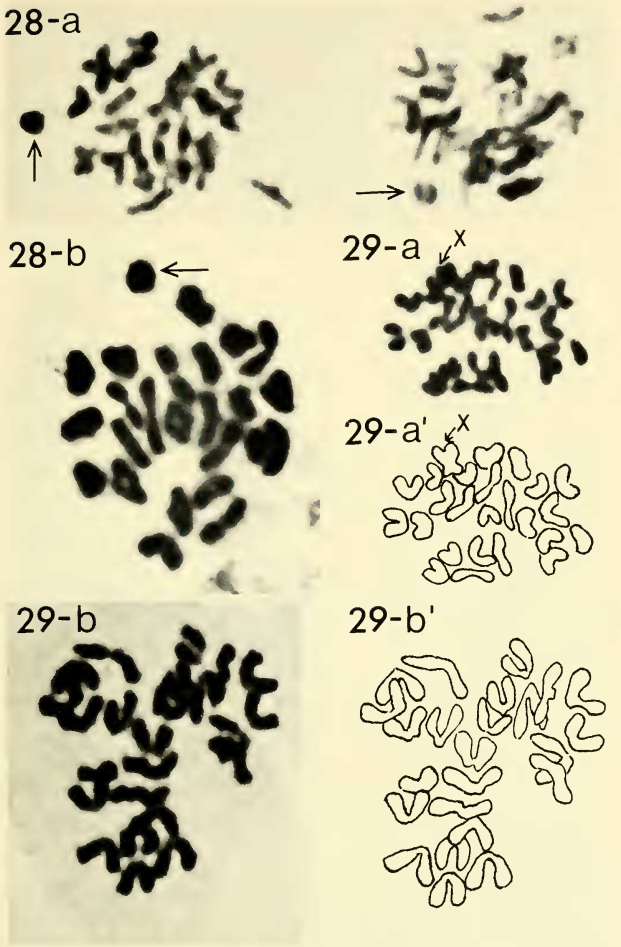



FIG. 28. Metaphase I of *Parvilux ingens* showing atypically behaving "X" univalent (a and b).

FIG. 29. Metaphase II of *Parvilux ingens*, (n = 25, a and a') with and the other (n = 24, b and b') without the "X".

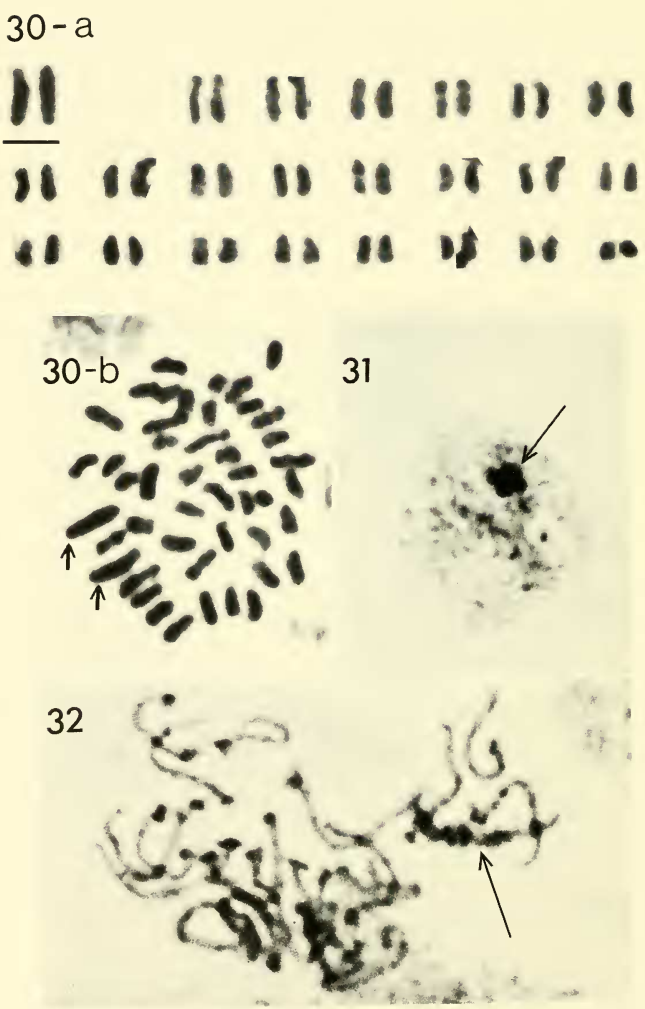



FIG. 30. Karyotype of *Scopelogadus mizolepis bispinosus* (2n=46). a. Idiogram. b. Metaphase plate corresponding to a.

FIG. 31. Preleptotene of *S. m. bispinosus* showing the presumed heterochromatic sex element (arrow).

FIG. 32. Pachytene of *S. m. bispinosus* showing a lampbrush-like "X-Y" bivalent (arrow).

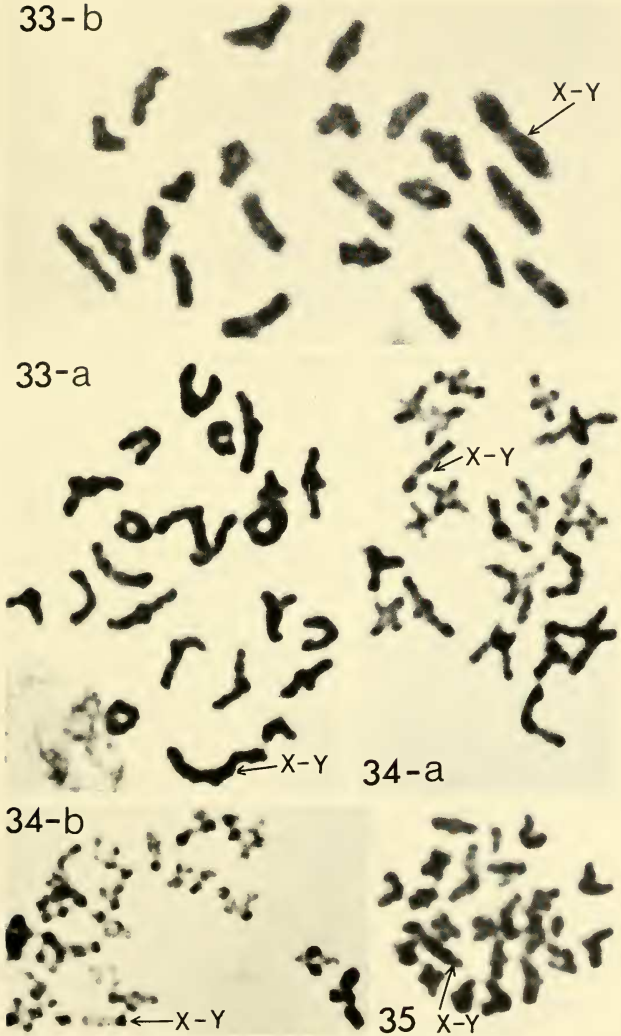



FIG. 33. Premetaphase I (a) and metaphase I (b) of *Scopelogadus mizolepis bispinosus*.

FIG. 34. Metaphase I (a and b) of *Scopeloberyx robustus* (2n=42, n=21) showing the heteromorphic "sex" bivalent (arrow).

FIG. 35. Metaphase I of *Melamphaes parvus* (2n=50, n=25) showing the heteromorphic "sex" bivalent (arrow).